Advice on West Coast rockfish harvest rates from Bayesian meta-analysis of stock-recruit relationships

Martin Dorn
Alaska Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
7600 Sand Point Way NE, BIN C15700
Seattle, WA 98115-0070

Abstract. Over the past two decades, rockfish populations off the west coast of the U.S. have declined sharply, leading to increasing concern about the sustainability of current harvest policies. In this paper, I develop a hierarchical Bayes model to jointly to estimate the stock-recruit relationships of rockfish stocks in the eastern Pacific. Stock-recruit curves for individual stocks are linked using a prior distribution for the "steepness" parameter of the Beverton-Holt S-R curve, defined as the expected recruitment at 20% of unfished biomass relative to unfished recruitment. The choice of a spawning biomass per recruit (SPR) harvest rate is considered a problem in decision theory, in which different options are evaluated in the presence of uncertainty in the stock-recruit relationship. Markov chain Monte Carlo (MCMC) sampling is used to obtain marginal distributions of variables of interest to management, such as the yield at a given SPR rate. A wide range of expected yield curves were obtained for different rockfish stocks. Pacific Ocean perch stocks in the Gulf of Alaska and the Aleutian Islands are apparently the most resilient stocks, with maximum expected yield SPR rates greater than F30% for all model configurations. In contrast, the maximum expected yield SPR rate for the West Coast stock of Pacific Ocean perch was lower than F70%. The SPR rates at MSY for other stocks were clustered between 40-60%, and depended on both on the S-R model (Beverton-Holt or Ricker) and the model for recruitment variability (lognormal or gamma). An F40% harvest rate, the current default harvest rate for rockfish, exceeded the estimated FMSY rate for all West Coast rockfish stocks with the exception of black rockfish.

The rockfishes (*Sebastes* spp.) are large number of closely related species found primarily in the eastern Pacific, with about 71 species distributed from the Gulf of California to the Bering Sea. Over the past two decades, rockfish populations off the west coast of the U.S. have declined sharply (Ralston 1998). Declines were anticipated for stocks that had been lightly exploited previously (e.g., widow rockfish and yellowtail rockfish), since even sustainable harvesting would reduce stocks by one-half to two-thirds from unfished levels. However, several stocks have shown little evidence of stabilizing at these lower levels. Age-structured assessments show declines in recruitment as the spawning stock has declined, suggesting that compensatory processes in early life history may be unusually weak compared to other groundfish species. Moreover, the West Coast Pacific Ocean perch stocks, which were reduced to low abundance by overfishing in the 1960's and 1970's, have been slow to rebuild. These factors have led to increasing concern about the sustainability of current harvest policies for rockfish.

West Coast rockfish are managed by the Pacific Fisheries Management Council (PFMC) using a Fishery Management Plan (FMP) developed to meet the requirements of Magnuson-Stevens Fisheries Management Act and implementation guidelines to established by National Marine Fisheries Service. The FMP includes definitions of 1) an MSY rule (FMSY) that maximizes long-term average yields; 2) an OY rule that reduces fishing mortality when stock size is below BMSY; 3) and guidelines for reducing OY to account for uncertainty in stock status. Since obtaining a reliable estimate of FMSY for particular fish stock is difficult, proxies are established for FMSY and BMSY based on spawning biomass per recruit (SPR).

In 1990, an FMSY proxy of F35% (the fishing mortality rate that reduces SPR to 35% of unfished) was adopted for all West Coast groundfish based on work by Clark (1990). He showed that a large fraction of the potential yield from a typical groundfish stock could be obtained at this SPR rate across a discrete set of plausible stock-recruit relationships, including both Ricker and Beverton-Holt forms. In 1997, the FMSY proxy for rockfish was reduced to F40% based on several considerations, including concerns about the continuing decline of rockfish stocks and further work by Clark (1993) showing that the F40% harvest rate would reduce the probability of low biomass if recruitment is highly variable or autocorrelated.

A harvest rate based on spawning biomass per recruit is explicitly intended to protect stocks from recruitment overfishing. SPR-based harvest rates will also harvest unproductive stocks at lower rates than productive stocks, similar to an F=M strategy (Clark 1990). However, rockfish as a group possess unique characteristics that distinguish them from other groundfish, including scarcity, ovi-viviparity, sex differences in growth and mortality, long life-spans, and high recruitment variability. It is not clear that the general advice of Clark (1990, 1993) provides sufficient guidance for establishing an FMSY proxy for rockfish.

In this paper, I develop a hierarchical Bayes model jointly to estimate the stock-recruit (S-R) relationships of all rockfish stocks in the eastern Pacific for which stock-recruit data are available. Hierarchical models were used by Hilborn and Liermann (1997) to assess depensation in S-R relationships. In a similar approach, Myers et al (1997) used linear mixed-models in a meta-analysis of S-R data to estimate the slope at the origin of the stock recruit relationship. This work focused on characterizing the mean and variance of various properties of the stock recruit relationship in broad taxonomic groupings, i.e., the strength of depensation, or the slope at the origin. I extend this work by considering management decisions, such as the choice of a SPR harvest rate, as a problem in decision theory, in which different options are evaluated in the presence of uncertainty in the stock-recruit relationship (Thompson 1992). Markov chain Monte Carlo (MCMC) sampling is used to obtain marginal distributions of variables of interest to management, such as the yield at a given SPR rate.

Subsequent sections of the paper are:

- ► Parameterizing the B-H curve to allow comparisons between stocks
- Developing a hierarchical Bayes model
- Likelihoods, priors, and hyperpriors for parameters in the joint posterior distribution
- Using the MCMC algorithm to obtain the marginal distributions of S-R parameters
- Using decision theory to evaluate SPR harvest rates
- ► Modifications (Ricker S-R curve, gamma error)
- Data Sources
- Results
- Discussion

Methods

Re-parameterizing the Beverton-Holt curve

The customary formulation of the Beverton-Holt curve for a single stock is

$$R = \frac{aS}{b + S} ,$$

where R is the recruitment produced by spawning biomass S (or another proxy of the annual spawning production of the stock). For a hierarchical model it is convenient to parameterize the Beverton-Holt curve by R_0 , the expected recruitment for an unfished stock size of S_0 , and a parameter that measures the resiliency of the stock, h, defined as the proportion of R_0 that recruits when the stock is reduced to 20% of unfished biomass (i.e., the "steepness" parameter of Mace and Doonan (1988)),

$$hR_0 = \frac{a(0.2 S_0)}{b + 0.2 S_0}.$$

For a steepness of 0.2, recruits are a linear function of spawners. For a steepness of 1.0, recruitment is independent of spawning biomass. The Beverton-Holt curve with parameters R_0 and h is

$$R = \frac{0.8R_0hS}{0.2R_0\varphi_0(1-h) + (h-0.2)S}.$$

where $S_0 = \varphi_0 R_0$, and φ_0 is spawning biomass per recruit for an unfished stock, which is estimated independently using conventional spawning biomass per recruit equations (Gabriel et al. 1989).

The problem of jointly estimating the stock-recruitment parameters for a taxon is addressed by modeling the relationships (if any) between the R_0 and h for the individual stocks using hierarchical priors—that is, by using probability distributions to describe the mean and variance of those parameters within the taxon. I do not develop a hierarchical prior for R_0 since it measures the carrying capacity of the habitat occupied by the stock, and would be unrelated between stocks except to the extent that the habitats they occupy are similar.

The similarity of stocks within a taxon in their response to harvesting was modeled by assuming the logit of h_k , the steepness parameter for the kth stock, was normally distributed (after rescaling h_k into the interval (0,1)),

$$\beta_k = \log \left(\frac{h_k - 0.2}{1 - h_k} \right) , \beta_k \sim N(\mu, \tau^2) .$$

For h_k in the interval (0.2,1.0), the logit β_k ranges from $-\infty$ to $+\infty$.

Bayesian hierarchical modeling

A Bayesian hierarchical model describes the joint posterior distribution of the parameters with 1) the likelihood (the probability of the data given the parameters), 2) the prior (the probability distribution of the parameters), 3) and the hyperprior (the probability distribution of the parameters in the prior) (Gelman et al. 1995). The prior models characteristics of a parameter (i.e., the mean and variance) in a population, while the hyperprior plays the role usually associated with the prior in Bayesian analysis. It quantifies prior beliefs about the parameters in the prior. A diffuse hyperprior can be used to reflect ignorance about these parameters.

A hierarchical model consists of conditional probability distributions that link data, Z, to parameters, Θ , and parameters to hyperparameters, Φ . The prior joint distribution of the parameters and hyperparameters is

$$p(\Theta, \Phi) = p(\Theta|\Phi) p(\Phi)$$

The joint posterior distribution is obtained by Bayes' rule,

$$p(\Theta, \Phi|Z) \propto p(Z|\Theta, \Phi) \ p(\Theta, \Phi)$$

$$= p(Z|\Theta, \Phi) \ p(\Theta|\Phi) \ p(\Phi)$$

$$= p(Z|\Theta) \ p(\Theta|\Phi) \ p(\Phi)$$

with the last equality because the data depend the hyperprior only through the prior. The resulting joint posterior distribution is the product of the likelihood, the prior, and the hyperprior, described in more detail below. The logarithm of joint posterior distribution, consisting of a sum of log likelihoods, is typically used in posterior mode-finding routines and in MCMC sampling.

Likelihood $p(Z|\Theta)$ —The assumption of lognormal errors in S-R models is based on both theoretical considerations (Hilborn and Walters 1996) and empirical studies (Peterman 1996, Myers 1995). A lognormal probability density for recruitment is

$$p(R|\hat{R}(S,R_0,\beta),\sigma^2) = \frac{1}{R\sqrt{2\pi}\sigma} \exp\left[-\frac{1}{2\sigma^2} \left(\log R - \log \hat{R} + \frac{\sigma^2}{2}\right)^2\right],$$

where $\hat{R}(S, R_0, \beta)$ is the expected recruitment as a function of the S-R parameters and spawning biomass, and σ^2 is a shape parameter. Note that the mean of the lognormal variate is used here rather than the usual parameterization with the median, $m = \mu \exp(-\sigma^2/2)$. To model relationships in S-R curves between stocks in a meaningful way, the S-R parameters should govern the shape the mean curve rather than the median curve. This is particularly important when the variability around the curve differs substantially between stocks, as is the case for rockfish. For K stocks with multiple observations on each stock, the negative log likelihood is proportional to

$$-\log L_1 = \sum_{k=1}^K \sum_i \frac{\left(\log R_{ik} - \log \hat{R}_{ik}(S_{ik}, R_{0k}, \beta_k) + \sigma_k^2/2\right)^2}{2\sigma_k^2} + n_k \log \sigma_k.$$

Note that I assume no correlation in recruitment and no errors in spawning biomass. These simplifying assumptions are unlikely to be true, and should provoke a healthy scepticism concerning the results.

Prior $p(\Theta|\Phi)$ —The hierarchical structure was developed only for the "steepness" parameters, h_k . For σ_k , a locally uniform prior on a log scale was used. A weak non-hierarchical prior was used for R_0 to prevent the estimate from deviating too much from the recruitment observed at high spawning biomass. This prior had a minor effect on the posterior mode, but curbed the tendency to sample extremely large values of R_0 from the posterior distribution during MCMC sampling for stocks with uninformative S-R data. The prior mean for the kth stock, \hat{R}_{0k} , was set to the average recruitment at spawning biomass > median observed spawning biomass, and deviations from this prior were assumed normal, with CV = 2.0.

The negative log likelihood for the prior is proportional to

$$-\log L_2 = \frac{1}{2\tau^2} \sum (\beta_k - \mu)^2 + K \tau + \frac{1}{2} \sum \left(\frac{R_{0k} - \hat{R}_{0k}}{CV \cdot \hat{R}_{0k}} \right)^2.$$

Hyperprior $p(\Phi)$ —The hyperprior specifies the probability distributions for μ and τ^2 . When possible, uninformative hyperpriors should be used to let the posterior distribution of μ and τ^2 reflect the information about these parameters contained in data. For μ , a locally uniform prior was used to reflect the lack of knowledge about this parameter. Obtain a suitable prior for τ^2 , however, was difficult. A common uninformative prior for a scale parameter is to assume that it is uniform on a log scale, i.e. $\log(\tau) \propto 1$. In a hierarchical model, however, this assumption produces an improper posterior (Gelman et al. 1995). Gelman et al. (1995) suggest using $\tau \propto 1$, which worked well for some model configurations and data sets. For more restricted data sets, using a uniform prior for τ shrank the distribution of steepness to zero, indicating no difference between stocks. Using a uniform prior on τ also did not constrain the β_k 's sufficiently for some model configurations to obtain well-behaved MCMC samples from the posterior distribution. In these cases, I assumed that the prior for τ^2 followed an scaled inverse Chi-square distribution, the conjugate prior for a normal distribution scale parameter. The negative log likelihood for a scaled inverse Chi-square distribution is proportional to

$$-\log L_3 = (v/2+1) \log \tau^2 + \frac{vs^2}{2\tau^2},$$

with parameters v and s^2 . This prior distribution can be regarded as providing the same information about τ^2 as v prior observations with a variance of s^2 (Gelman et al. 1995).

The log joint posterior distribution is the sum of the log likelihood, the prior log likelihood, and the hyperprior log likelihood,

$$L = \log L_1 + \log L_2 + \log L_3.$$

The posterior mode of the total log likelihood was obtained using the AD model builder nonlinear optimization software (Otter Research 1996).

Obtaining posterior distributions using the Markov Chain Monte Carlo algorithm

To estimate FMSY for a stock of interest, the marginal posterior distribution of the stock recruit parameters for that stock is required, which can be obtained by integrating joint posterior distribution with respect to the other parameters. Rather than evaluating this integral analytically, I used the Markov chain Monte Carlo (MCMC) algorithm to obtain random samples from the joint distribution. From these samples it is an easy matter to obtain empirical histograms that approximate the marginal distribution of any parameter of interest.

The MCMC algorithm simulates a Markov chain of random samples (i.e., each sample is conditionally dependent on the preceding sample) whose stationary distribution is the joint posterior distribution. The basic steps of the algorithm are: 1) draw an initial sample from the posterior distribution; 2) generate a candidate for the next sample using a random jumping distribution from the current sample; 3) calculate the importance ratio, r, from the value of the joint posterior distribution at the current sample and the candidate sample; 4) if r is greater than one, accept the sample; 4) if r is less than one, accept or reject the candidate sample with probability r. 5) begin the next cycle at step 2. Gelman (1995) provides a good introduction to MCMC methods, and documentation of Hastings-Metropolis algorithm as implemented in AD model builder is at $\frac{http://otter-rsch.com/cc/cctoc.html$.

Decision-theoretic estimates of FMSY

Let $h_{(C)}$, $R_{0(C)}$ be a sample of the stock recruit parameters for stock of interest from the joint posterior distribution generated by MCMC algorithm. For each sample, the equilibrium recruitment $R^{EQ}(p)$ is obtained for a sequence of SPR rates p,

$$R^{EQ}(p) = \max \left(0, R_{0(C)} \frac{0.8 h_{(C)} p - 0.2(1 - h_{(C)})}{p(h_{(C)} - 0.2)} \right).$$

Some combinations of SPR rate and sampled stock recruit parameters result in negative equilibrium recruitment indicating that the SPR rate is not sustainable--hence the use of the *max* function in the above equation.

Equilibrium yield, $Y^{EQ}(p)$, and equilibrium spawning biomass, $S^{EQ}(p)$, at SPR rate p are

$$Y^{EQ}(p) = \eta_p R^{EQ}(p) ,$$

$$S^{EQ}(p) = p \varphi_0 R^{EQ}(p)$$
,

where η_p is the yield per recruit.

Risk aversion was explored by defining a loss function, the negative of which measures the societal benefits of the yield from the fishery, i.e., the "utility." From decision theoretic perspective, FMSY can be regarded as the fishing mortality rate that minimizes risk, where risk is the expected loss. Thompson (1992) proposed a general loss function for fishery yield as

$$l(Y) = \frac{1 - Y^{\lambda}}{\lambda} ,$$

where λ is used to control risk aversion. Linear loss is obtained when $\lambda=1$, while the logarithmic

loss is obtained in the limit as λ approaches zero. A linear loss function implies a risk-neutral approach, such that the expected yield is maximized, while any value of $\lambda < 1$ implies risk aversion. Although logarithmic loss is often used as a default risk-averse approach, using it in this problem would exclude any SPR rate with a non-zero probability of zero yield, implying extreme risk aversion. Instead, I use $\lambda = \frac{1}{2}$ as an example of a risk-averse approach, which corresponds to maximizing the expected square root of yield.

A decision-theoretic estimate of the SPR rate at FMSY is

$$SPR_{FMSY} = \min_{p} E[l(Y^{EQ}(p))]$$

The expected loss at a particular fishing mortality is obtained by averaging the loss associated with the equilibrium yield for each of the MCMC samples drawn from the joint posterior distribution. Of course, the relationship of the SPR rate to yield and risk is also of interest, in addition to the point estimates.

Modifications

The Beverton-Holt curve with lognormal errors can be replaced with other stock recruit relationships or alternative error models in the hierarchical model. Two important alternatives to consider are the Ricker S-R model and gamma errors.

Ricker S-R model

The standard form of the Ricker model is

$$R = aS \exp(-bS)$$

Kimura (1990) re-parameterized the Ricker curve in relation to R_0 , the expected recruitment for an unfished stock size of S_0 , and a curvature parameter, α . The Ricker curve with parameters R_0 and α is

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$$R = \frac{S}{\varphi_0} \exp \left[\alpha \left(1 - \frac{S}{R_0 \varphi_0} \right) \right].$$

Note that e^{α} is the potential increase in reproductive success relative to an unfished stock, so that additive changes in α imply multiplicative changes in reproductive success at low stock size. Steepness is not a useful concept for the Ricker model because recruitment at 20% of unfished biomass can be greater than unfished (steepness >1). I modeled the similarity of stocks in their response to harvesting by assuming that the curvature parameter for the kth stock was normally distributed.

$$\alpha_{\nu} \sim N(\mu, \tau^2)$$
.

Hyperpriors for μ and τ^2 were the same as those developed for the Beverton-Holt curve.

Equilibrium recruitment for the Ricker curve is

$$R^{EQ}(p) = \frac{R_0}{p} \left(1 + \frac{\log p}{\alpha} \right) .$$

Gamma likelihood

Myers et al.(in press) recommend the gamma distribution as an important alternative to lognormal distribution for recruitment variability. The gamma distribution parameterized by expected recruitment, \hat{R} , and a shape parameter, v, is

$$p(R|\hat{R}(S,R_0,\beta),\nu) = \frac{1}{\Gamma(\nu)} \left(\frac{\nu}{\hat{R}}\right)^{\nu} R^{\nu-1} \exp\left(-\frac{\nu R}{\hat{R}}\right)$$

Data sources

Stock-recruit data were obtained for 11 rockfish stocks in the eastern Pacific (Table 1). Sources included stock assessments published by PFMC, North Pacific Fisheries Management Council, Department of Fisheries and Oceans, and the Myers et al. (1995) database. A decision was made to be inclusive as possible when assembling the S-R data to reduce the potential for bias due to subjective selection criteria (Englund et al. 1999). An appendix provides a complete list of sources and documents the rationale for choosing a particular scenario when the assessment carried forward several scenarios. Assessment authors were also contacted personally to help resolve discrepancies and provide additional information. Although rockfish assessments are among the most technically advanced and comprehensive, all are highly uncertain due to the infrequent survey schedule off the West Coast and Alaska and because of the fundamental difficulty of surveying highly-aggregated fish populations that inhabit rocky areas.

Stock-recruit data from age-structured models for northern rockfish and the "Coastal" yellowtail rockfish stock in northern British Columbia were not used the meta-analysis because assessment authors considered the models preliminary, and noted model results that were considered implausible. Although a separate assessment was conducted for a putative "southern" canary rockfish stock in 1999 (Williams et al. 1999), the biomass and recruitment estimates from this assessment were added to the time series for the northern stock to reflect the assessment author's conclusion that canary rockfish in this area probably did not constitute a separate stock.

In addition to the stock-recruit data, life history and fishery selectivity information for each stock was used to estimate SPR and yield per recruit. Population response to harvesting on a per recruit basis can be compactly characterized by 1) the spawning biomass per recruit for an unfished stock, φ_0 , 2) a vector of yield per recruit (kg) as a function of the proportion of unfished SPR, η_p , where p=1.00,0.99,0.98,...,0.10 (Fig. 1). Note that the units of spawning biomass are unimportant as long as the estimates of stock size are calculated the same way.

Results

Figure 2 shows stock-recruit data for each stock and the estimated S-R relationships based on posterior mode parameter values for two Beverton-Holt curves with a lognormal error distribution. For the first curve, the S-R parameters for each stock are estimated independently, while for the second curve the hierarchical model is used to link the steepness parameters for the stocks. For all Beverton-Holt curves, a weakly informative hyperprior (inverse Chi-square distribution with parameters $\nu = 10$ and $s^2 = 0.5$) was used for τ^2 . When each stock is considered independently, a steepness of 1.0 is estimated for five of the 11 stocks (chillipepper rockfish, black

rockfish, and the Pacific Ocean perch stocks in Goose Island Gully, Gulf of Alaska, and the Aleutian Islands), implying that recruitment is unrelated to stock size. For the hierarchical model, a more plausible stock-recruit curve is estimated for these stocks, and all posterior mode estimates are shifted toward the overall average steepness of about 0.6 (Fig. 3).

Marginal posterior densities for h_k were obtained by subsampling every 200th sample of the joint posterior distribution from 500,000 cycles of the MCMC algorithm after an initial burn-in of 50,000 cycles. Empirical histograms representing the marginal posterior distributions of h_k are shown in Figure 4. The marginal posterior distributions of h_k for several stocks are consistently different from the rest. The West Coast stock of Pacific Ocean Perch shows a low posterior mode for steepness, suggesting low resilience to harvesting. Pacific Ocean Perch stocks north of Vancouver Island appear to be more resilient than other rockfish stocks to the south. The West Coast rockfish with informative stock-recruit data, i.e., widow, canary, and yellowtail rockfish, showed posterior modes in the middle of the range (0.5-0.7).

Posterior mode S-R curves for Beverton-Holt and Ricker models were similar, and both functional forms adequately described the mean relationship between stock size and recruitment (Fig. 5). The Ricker model consistently estimated a lower initial slope, but predicted higher recruitment at intermediate stock sizes. Ricker curves for the apparently more resilient stocks (i.e., Goose Island Gully Pacific Ocean perch) predict decreasing recruitment at high size, which is not evident in the data. For the less resilient stocks (i.e., widow rockfish), the Ricker curve closely tracks the asymptotic Beverton-Holt curve.

Lognormal and gamma error models also resulted in similar posterior mode S-R curves (Fig. 5). However, expected recruitment at high stock size was lower for the gamma error model. For widow rockfish, the gamma error model estimated a lower steepness than the lognormal model, resulting in a predicted S-R curve that more closely passes though the cluster of points at 100-200 units of spawning output. Log likelihoods at the posterior mode provide an overall indication of the comparative fits of different models, though from a Bayesian perspective the full posterior distribution of the parameters is main interest. Log likelihoods for the different stock recruit functions and error models are presented in Table 2. Overall, the log likelihoods for the Beverton-Holt model were higher than the Ricker model, with most of the differences attributable to the more resilient Pacific Ocean perch stocks (Table 2). Log likelihoods for the lognormal error model were slightly higher than the gamma error model.

To obtain a posterior predictive distribution for β_k (i.e., the distribution for an unobserved stock), it is necessary to integrate over μ and τ , the parameters that govern the distribution of β_k in the joint posterior distribution. This was done by augmenting the vector of β_k 's in the

hierarchical prior with an additional element with no associated S-R data, and using MCMC sampling to obtain the posterior distribution of that element. A posterior predictive distribution was obtained for α_{ι} in the Ricker model in the same way.

Figure 6 compares these posterior predictive distributions with a normal distribution in the same parameter space inferred from the discrete set of S-R relationships considered by Clark (1990). Clark initially considered a set of five S-R curves for the Beverton-Holt and Ricker models. These curves differed by the potential increase in reproductive success (R/S at the origin) relative to an unfished stock (R_0/S_0). Consideration was then narrowed to the three curves in the middle. Potential increases in reproductive success by factors of 4, 8, and 16 were considered plausible, while factors of two and 32 were considered implausible. The inferred distribution was centered on a reproductive success factor of eight, and scaled so that reproductive success factors of two and 32 were located on the upper and low tails.

Figure 6 shows that the posterior predictive distributions are wider than the range considered by Clark (1990). Furthermore, the posterior mode estimates for most rockfish are lower than the mean of Clark's implied distribution, particularly for the Ricker model, suggesting that the range of S-R relationships considered by Clark may be too optimistic for rockfish.

For each SPR harvest rate, MCMC sampling generates a probability distribution that describes the effect of uncertainty in the stock-recruit relationship on equilibrium yield. Figure 7 shows this distribution for chillipepper rockfish; other stocks show similar patterns. The expected yield (the average of the distribution of yield) increases, reaches a maximum, and then declines--as would occur for a fixed parameter S-R relationship. However, parameter uncertainty in the S-R relationship affects distribution of yield in ways that are important to consider. The CV of yield is constant when the harvest rate is below the SPR rate where yield is maximized (~F41% for chillipepper rockfish), then increases as the harvest rate increases, indicating that uncertainty in yield increases as the harvest rate increases. At harvest rates higher than FMSY, yield has a bimodal distribution: either large equilibrium yields are possible, or the harvest rate results in stock collapse. The probability of zero yield (stock collapse) increases monotonically from less than 0.05 at FMSY to 0.63 at F10%.

A wide range of expected yield curves is obtained for different rockfish stocks (Fig. 8). Pacific Ocean perch stocks in the Aleutian Islands and Gulf of Alaska are apparently the most resilient stocks, with maximum expected yield SPR rates greater than F30% for all model configurations. The West Coast stock of Pacific Ocean perch is at the other end of the range, with maximum expected yield SPR rates lower than F70%. The SPR rates at MSY for other stocks were clustered between 40-60%, and depended on both on the S-R model (Beverton-Holt

or Ricker) and the model for recruitment variability (lognormal or gamma). A general ordering of models from the highest harvest rate at MSY to the lowest is 1) Beverton-Holt with lognormal error, 2) Ricker with lognormal error, 3) Beverton-Holt with gamma error, 4) Ricker with gamma error. Risk averse estimates of FMSY (maximum square root yield) were 0-10 percentage points higher in SPR than risk neutral estimates (average difference 4.1 percentage points). Results are summarized in the following table, where the maximum for a group of stocks was obtained by scaling each yield curve relative to its maximum, and then averaging across stocks.

Table. SPR harvest rate at MSY for risk neutral (maximum expected yield) and risk averse (maximum square root yield) loss functions for all rockfish stocks and for West Coast rockfish stocks excluding Pacific Ocean perch.

S-R Model	Recruitment error model	All	stocks	West Coast stocks except POP			
		Risk-neutral	Risk-averse	Risk-neutral	Risk-averse		
Beverton-Holt	Lognormal	44	54	45	47		
	Gamma	56	62	56	60		
Ricker	Lognormal	54	59	54	57		
	Gamma	62	65	67	67		

More detailed information is presented in Figure 9, which shows the expected yield for each stock for a range of SPR harvest rates.

Discussion

Uncertainty permeates the problem of harvest rate estimation, perhaps more so than in any other aspect of fisheries science. Bayesian methods, like the hierarchical models developed in this paper, are able to deal with uncertainty in a rigorous way. Nevertheless, there are potentially important sources of bias and uncertainty that could not be addressed with these methods. Those sources of uncertainty are discussed in more detail below. First, though, a warning about the provisional nature of any conclusions seems appropriate—and suggestions about how these results should be used in deliberations about target harvest rates. I do not recommend adopting the risk-neutral or risk-averse point estimate of FMSY for any stock, particularly for those with apparently extreme stock-recruit relationships. The results should be used in a more advisory manner to 1)

determine whether the current harvest policy requires modification, and 2) make an informed decision about the direction and magnitude of that change. This decision should be guided by (but not completely determined) an evaluation of whether a proposed SPR harvest rate is less than FMSY and whether a large percent of the potential yield can be obtained at that harvest rate for a group of stocks, based on the meta-analysis of stock-recruit data.

Results suggest that SPR harvest rates in the F40-60% range should be considered for West Coast rockfish. An F40% harvest rate exceeded the FMSY rate for all West Coast stocks and all sets of model assumption except for black rockfish using the Beverton-Holt model. After excluding West Coast Pacific Ocean perch, only four of the 24 combinations of stock and stock-recruit model assumptions indicated that FMSY was higher than F60%. The West Coast stock of Pacific Ocean Perch had lowest estimated steepness of all rockfish stocks considered, suggesting that the stock's compensatory response to harvesting is unusually weak. A lower harvest rate may be advisable for this stock.

Although Canadian and Alaskan rockfish stocks were not specifically an objective of this research, a few comments follow. For the Goose Island Gully Pacific Ocean perch stock, the current harvest policy of F=M corresponds to an F49% harvest rate (Richards et al. 1997). Although the FMSY rate was higher, the loss of long-term yield at an F=M policy is probably less than 5%, and could be considered as risk-averse harvest policy. For Pacific Ocean perch stocks in Alaska, a default F40% harvest policy is used. Hierarchical model results for all model configurations suggest that this rate is lower than FMSY for both the Gulf of Alaska and the Aleutian Island stocks. The loss of long-term yield for the Gulf of Alaska stock was approximately 12% at an F40% harvest rate, and around 7% for the Aleutian Islands stock for the Beverton-Holt model. The eastern Bering Sea stock has been slower to rebuild than other Alaska stocks, and may be less resilient to harvesting. Hierarchical model results suggest that harvest rates in the F45-50% range may be more appropriate than the current F40% policy.

Pacific Ocean Perch is represented by five stocks from south to north as follows: West Coast, Goose Island Gully, Gulf of Alaska, Aleutian Islands, and Eastern Bering Sea. All were severely overfished by distant water fleets in the 1960's and 1970's. It is interesting to note that Pacific Ocean perch stocks towards the center of the distribution have rebuilt strongly, and have S-R curves with high steepness. Stocks at the northern and southern limit of the distribution, the West Coast and eastern Bering Sea stocks, have been slow to rebuild, and have S-R curves with low steepness. The abundance of these peripheral stocks may be governed more by environmental conditions that expand or shrink favorable habitat, rather than density-dependent processes, suggesting that sustainable harvesting of these stocks may be difficult.

The models developed in this paper treat stock and recruitment estimates from assessment models as though they were data. Although this is a standard assumption for stock-recruit analyses, it is important to consider how this assumption could affect the results. Rockfish assessments are data poor, and equilibrium assumptions are often made to initialize the numbers at age matrix. The stock-recruit estimates produced by such models are highly uncertain. Because biomass is linked to earlier recruitment in an assessment model, a trend in stock size caused by a spurious survey index that may bias the estimates of FMSY. One striking example is the yellowtail rockfish assessment (Tagart et al. 1997), which carried forward two scenarios that differed in the types of fishery-independent information used to tune the model. The estimated steepness in the stock-recruit relationship depends strongly on which scenario is considered correct (Fig. 10).

Another potential source of bias in estimating S-R curves is the bias that results from the time series nature of stock recruit data. This bias is caused because high recruitments produce high spawning biomass, and low recruitments produce low spawning biomass. Consequently, the stock sizes at which recruitments are observed are not controlled variables, as is required for S-R parameter estimates to be unbiased. A thorough discussion of time series bias can be found in Hilborn and Walters (1992). Usually this bias has the effect of flattening the S-R curve, so that stocks appear to be more resilient to harvesting than they are. Because most rockfish stocks have been fished from pristine to low levels without reversals in the biomass trend, rockfish S-R parameters may be relatively unaffected by this bias. The estimates of high steepness for the Pacific Ocean perch stocks that have experienced a reversal in biomass trend are questionable because of time series bias.

Since the analysis presented in this paper focuses on equilibrium yield, it does not assess the effect of recruitment variability on the stability of the stock and associated yield. This may not be a serious shortcoming because as Clark (1985) notes "simply passing from a deterministic model to a related stochastic model is likely to have very little quantitative effect on the outcome of an optimization analysis." However, a lower fishing mortality rate would reduce fluctuations in abundance and yield caused by recruitment variability. Estimates of FMSY do not consider the potential benefits to the stock and the fishing industry that a lower harvest rate would have in reducing variability.

The use of maximum expected square root yield as a risk averse objective is arbitrary, though reasonable. It was used simply as an example of how to obtain a harvest rate that is formally risk averse in the presence of uncertainty in the S-R relationship. For the risk averse loss function considered here, the SPR harvest rate was increased average of four percentage points from the risk neutral SPR rate. It is important to note that the harvest control rule currently in

place for West Coast groundfish (the 40-10 rule) provides many of the same benefits of a risk averse constant harvest rate by reducing the harvest rate at low stock size.

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Thompson, G. G. 1992. A Bayesian approach to management advice when stock-recruitment parameters are uncertain. Fishery Bulletin. U.S. 90:561-573.

Figure Captions

- Figure 1. Yield per recruit (YPR) as a function of the percent unfished SPR for 11 eastern Pacific rockfish stocks.
- Figure 2. Stock recruit data for 11 eastern Pacific rockfish stocks. Two stock recruit curves are shown. The solid lines show the Beverton-Holt S-R curve based on the posterior mode from a Bayes hierarchical model. Dotted lines show the resulting curves when each S-R relationship is estimated separately.
- Figure 3. Posterior mode estimates of steepness, h_k , when each S-R relationship is estimated separately and for a Bayes hierarchical models for 11 eastern Pacific rockfish stocks.
- Figure 4. Marginal posterior distributions of steepness, h_k , for 11 rockfish stocks from a Bayes hierarchical model.
- Figure 5. Comparison of posterior mode S-R curves for different stock-recruit models (Beverton-Holt and Ricker) and different recruitment error distributions (lognormal and gamma) for widow rockfish and Goose Island Gully Pacific Ocean perch.
- Figure 6. Posterior predictive distribution of β_k for the Beverton-Holt model for an unobserved stock (top panel). The location of the posterior mode estimates of β_k for ten rockfish stocks are indicated on the distribution. Also shown is a distribution inferred from the discrete Beverton-Holt S-R curves (points indicated on the distribution) considered by Clark (1990). The bottom panel shows the posterior predictive distribution of α_k for the Ricker model.
- Figure 7. Distribution of equilibrium yield obtained by MCMC sampling as a function of the SPR harvest rate for chillipepper rockfish. The bottom panel shows the probability of zero yield.
- Figure 8. Relative expected equilibrium yield as a function of the SPR harvest rate for different S-R models (Beverton-Holt and Ricker) and different error distributions (lognormal and gamma) for ten rockfish stocks.
- Figure 9. Relative expected yield at SPR harvest rates from F35%-60% for ten rockfish stocks. The results from four models are shown for each stock (from left to right: Beverton-Holtlognormal, Beverton-Holt-gamma, Ricker-lognormal and Ricker-gamma). Solid bars indicate that the harvest rate is higher than SPR rate that maximizes expected yield.

Figure 10. S-R data and estimated Beverton-Holt S-R curves for two yellowtail rockfish assessment scenarios (models 3 and 8) in Tagart et al.(1997). The scenarios differed in the types of fishery-independent information used to tune the model (additional details are in Tagart et al. 1997).

Appendix: Stock-recruit data sources

Chillipepper Rockfish

Ralston, S., D. E. Pearson, and J. A. Reynolds. 1998. Status of the chillipepper rockfish in 1998. In: Status of the Pacific coast groundfish fishery through 1998 and recommended acceptable biological catches for 1999. Pacific Fishery Management Council, 2130 SW Fifth Ave., Suite 224, Portland, OR 97201

SPR = spawning multiplier * female numbers at age at start of year

Bocaccio Rockfish

MacCall, A, Ralston, S., D. Pearson, and E. Williams. Status of bocaccio off California in 1999 and outlook for the next millennium. In: Status of the Pacific coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000. Pacific Fishery Management Council, 2130 SW Fifth Ave., Suite 224, Portland, OR 97201

All recruitments less than 0.2 million were set to 0.2 million. This arbitrary adjustment changes the mean by less than 1%, but allows the lognormal error model to obtain reasonable results. Most extremely small bocaccio rockfish recruitments occur adjacent to strong year classes, and may be affected by the fixed transition matrices used by stock synthesis to convert length to age and for ageing error.

SPR = spawning multiplier * female numbers at age at start of year

Widow Rockfish

Ralston, S., D. E. Pearson. Status of the widow rockfish in 1997. In: Status of the Pacific coast groundfish fishery through 1997 and recommended acceptable biological catches for 1998. Pacific Fishery Management Council, 2130 SW Fifth Ave., Suite 224, Portland, OR 97201

SPR = female weight at age * female maturity * fecundity per gram body weight * female numbers at age at beginning of the year

Canary rockfish

Williams, E. H., S. Ralston, A. D. MacCall, D. Woodbury, and D. E. Pearson. 1999. Stock assessment of the canary rockfish resource in the waters off southern Oregon and California in 1999. Appendix to Status of the Pacific coast groundfish fishery through 1999 and recommended

acceptable biological catches for 2000. Pacific Fishery Management Council, 2130 SW Fifth Ave., Suite 224, Portland, OR 97201.

Crone, P. R., K.P. Piner, R.D. Methot, R.J. Conser, and T.L. Builder. 1999. Status of canary rockfish resource off Oregon and Washington in 1999. Appendix to Status of the Pacific coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000. Pacific Fishery Management Council, 2130 SW Fifth Ave., Suite 224, Portland, OR 97201.

Age-dependent natural mortality model (Scenario 1) was used because the STAR panel considered this model to be the most plausible (P. Crone pers. comm.)

SPR = female weight at age * female maturity* female numbers at age at beginning of the year

Stock and recruit data for the northern and southern stocks were combined for the meta-analysis because of the reservations expressed by the assessment author about whether the southern stock can be considered distinct from northern populations of canary rockfish.

Black Rockfish

Wallace, F.R. A. Hoffmann, and J. V. Tagart. 1999. Status of the black rockfish resource in 1999. In: Status of the Pacific coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000. Pacific Fishery Management Council, 2130 SW Fifth Ave., Suite 224, Portland, OR 97201.

SPR = female weight at age * female maturity* female numbers at age in February.

Yellowtail Rockfish

Tagart, J. V., J. N. Ianelli, A. Hoffman, and F.R. Wallace. 1997. Status of the yellowtail rockfish resource in 1997. In: Status of the Pacific coast groundfish fishery through 1997 and recommended acceptable biological catches for 1998. Pacific Fishery Management Council, 2130 SW Fifth Ave., Suite 224, Portland, OR 97201.

Results from Model 8 were used because the 1998 AFSC shelf survey showed higher yellowtail biomass consistent with Model 8.

SPR = female weight at age * female maturity* female numbers at age in April (0.25 of year).

Pacific Ocean Perch - West Coast

Ianelli, J. N. and M. Zimmerman. 1998. Slope rockfish stock assessment for the west coast of Canada in 1996 and recommended yields for 1997. Pacific Fishery Management Council, 2130 SW Fifth Ave., Suite 224, Portland, OR 97201.

Ianelli, J. N., D.H. Ito, and M. Wilkins. 1995. Status and future prospects for the Pacific ocean perch resource in waters off Washington and Oregon as assessed in 1995. In: Status of the Pacific coast groundfish fishery through 1995 and recommended acceptable biological catches for 1996. Pacific Fishery Management Council, 2130 SW Fifth Ave., Suite 224, Portland, OR 97201.

The base run assessment model contained a Bayesian prior on steepness, which would make the stock-recruit estimates unusable in a meta-analysis of steepness. J. Ianelli re-ran the model without a prior on steepness and provided the resulting biomass and recruitment time series (J. Ianelli pers. comm. 6/15/99).

SPR = female weight at age * female maturity* female numbers at age at beginning of year.

Pacific Ocean Perch - Goose Island Gully stock

Richards, L. J. and N. Olsen. 1996. Slope rockfish stock assessment for the west coast of Canada in 1996 and recommended yields for 1997. Can. Tech. Rep. Fish. Aquat. Sci. No. 2134: 91p.

Richards, L. J. 1994. Slope rockfishes, p. 230-287. In M. Stocker (ed.). Groundfish stock assessments for the west coast of Canada in 1993 and recommended yield options for 1994. Can. Tech. Rep. Fish. Aquat. Sci. No. 1975. 352 p.

The time series of recruitment in the Myers database is in units of millions of recruits at age 7, not in biomass as indicated in the documentation for Myers database (L. Richards pers. comm.) Maturity from Fig. 4.2.6, Selectivity from Fig 4.4.3., Weight at age from Table 9.14 in Richards (1994).

SPR = female weight at age * female maturity* female numbers at age at beginning of year + male weight at age * male maturity* male numbers at age at beginning of year. This is the only assessment that uses undifferentiated (M+F) spawning biomass.

Pacific Ocean Perch - Gulf of Alaska stock

Heifitz, J., J. N. Ianelli, D. M. Clausen, and J.T. Fujioka. 1999. Slope rockfish. In: Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska region. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

SPR = female weight at age * female maturity* female numbers at age in May.

Pacific Ocean Perch - Aleutian Island stock

Ito, D. H., P.D. Spencer, and J. N. Ianelli. 1999. Pacific Ocean Perch. In: Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Island regions. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

SPR = female weight at age * female maturity* female numbers at age at beginning of year.

Pacific Ocean Perch - Eastern Bering Sea stock

Ito, D. H., P.D. Spencer, and J. N. Ianelli. 1999. Pacific Ocean Perch. In: Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Island regions. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

SPR = female weight at age * female maturity* female numbers at age at beginning of year.

"Coastal" B.C. Yellowtail Rockfish

Stanley, R. and V. Haist. 1997. Shelf rockfish stock assessment for 1997 and recommended yield options for 1998. Canadian Stock Assessment Secretariat. Research Document 97/132.

Preliminary assessment model. S-R data not included in the analysis.

Northen Rockfish

Courtney, D.L., J. Heifetz, M.F. Sigler, and D.M. Clausen. 1999. Appendix 6-1: An agestructured model of northern rockfish, *Sebastes polyspinis*, recruitment and biomass in the Gulf of Alaska.. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

Preliminary assessment model. S-R data not included in the analysis.

Table 1. Eastern Pacific *Sebastes* stocks used in meta-analysis of stock recruit relationships. SPR is the annual reproductive output defined variously as total spawning biomass, female spawning biomass, or annual egg production (Assessment models: SS-age = Stock synthesis age-based model, SS-length = Stock synthesis length-based model, ADMB-age = AD model builder age-structured model, ADMB-length = AD model builder size-structured model.

			Assessment		No. of	Recr.		SPR at
Species	Stock	Code	model	Years	Yrs	Age	Average M	F = 0
S. goodei	West coast	CHILLIPEPPER	SS-length	1970-97	28	1	0.24	1.306
S. paucispinis	West coast	BOCACCIO	SS-length	1969-98	30	1	0.20	1.289
S. entomelas	West coast	WIDOW	SS-age	1970-96	27	1	0.15	7.753
S. pinniger	West coast	CANARY	SS-age /	1967-94	28	1	0.08	7.789
			ADMB-lengt	:h				
S. melanops	Wash N. Ore.	BLACK	ADMB-age	1986-92	7	6	0.28	1.21
S. flavidus	West coast	YELLOWTAIL	ADMB-age	1967-93	27	4	0.14	2.403
S. alutus	West coast	PERCHWUS	ADMB-age	1956-95	40	3	0.06	6.155
S. alutus	Goose Island Gully	PERCHGOOSE	ADMB-age	1963-88	26	3	0.05	18.144
S. alutus	Gulf of Alaska	PERCHGA	SS-age	1977-92	16	2	0.05	5.570
S. alutus	Aleutian Islands	PERCHAI	SS-age	1962-89	28	3	0.05	5.729
S. alutus	Eastern Bering Sea	PERCHEBS	SS-age	1960-96	37	3	0.05	5.482
Total					294			

Table 2. Posterior mode log likelihoods for different stock-recruit relationships (Beverton-Holt and Ricker) and different recruitment error distributions (lognormal and gamma) for a hierarchical model of rockfish stock-recruitment relationships.

	Beverton	ı-Holt	Ricker		
Stock	lognormal	gamma	lognormal	gamma	
CHILLIPEPPER	122.0	102.0	122.2	122.4	
_	-122.0	-123.2	-122.3	-123.4	
BOCACCIO	-58.4	-60.2	-58.4	-59.4	
WIDOW	-117.3	-117.2	-117.2	-117.0	
CANARY	-24.4	-24.2	-24.8	-24.7	
BLACK	-3.9	-3.9	-2.3	-1.9	
YELLOWTAIL	-77.2	-76.6	-77.1	-76.4	
PERCHWUS	-67.3	-68.4	-66.6	-67.9	
PERCHGOOSE	-70.8	-69.3	-71.3	-69.7	
PERCHGA	-78.7	-77.8	-78.8	-78.0	
PERCHAI	-132.9	-136.0	-135.9	-138.9	
PERCHEBS	-128.4	-130.6	-129.6	-132.9	
R ₀ prior	-45.3	-45.5	-45.0	-45.2	
Hierarchical prior	-11.8	-14.3	-9.0	-10.4	
Hyperprior	-0.8	-1.0	-0.8	-0.8	
T 1	020.2	0.40.7	020.2	0.46.7	
Total	-939.3	-948.5	-939.2	-946.5	

Table 3. SPR fishing mortality rates that reduce equilibrium spawning biomass to 40% and 50% of unfished spawning biomass (B40%) for 11 Eastern Pacific Sebastes stocks based on posterior marginal means from a hierarchical meta-analysis of rockfish stock-recruitment relationships.

	SPR at B40% equilibrium			SPR at B50% equilibrium				
	BH-	BH-	Ricker-	Ricker-	BH-	ВН-	Ricker-	Ricker-
Stock	lognormal	gamma	lognormal	gamma	lognormal	gamma	lognormal	gamma
CHILLIPEPPER	51	56	56	60	59	63	62	67
BOCACCIO	54	70	53	75	62	76	60	80
WIDOW	53	63	56	65	61	69	62	70
CANARY	53	55	48	49	61	62	55	56
BLACK	49	50	44	45	58	59	51	51
YELLOWTAIL	51	53	55	56	59	61	61	62
PERCHWUS	69	72	69	71	75	77	78	75
PERCHGOOSE	48	47	41	40	57	56	48	46
PERCHGA	43	43	19	19	52	52	25	25
PERCHAI	43	44	27	28	53	53	34	35
PERCHEBS	49	48	45	42	58	56	52	49
Median	51	53	48	49	59	61	55	56

	Percent of MSY at B40%			Percent of MSY at B50%				
	BH-	BH-	Ricker-	Ricker-	BH-	BH-	Ricker-	Ricker-
Stock	lognormal	gamma	lognormal	gamma	lognormal	gamma	lognormal	gamma
CHILLIPEPPER	95%	97%	100%	100%	86%	89%	98%	98%
BOCACCIO	98%	100%	100%	100%	90%	96%	95%	94%
WIDOW	96%	99%	100%	99%	86%	93%	98%	99%
CANARY	100%	100%	98%	98%	95%	96%	99%	99%
BLACK	93%	95%	100%	99%	82%	86%	95%	95%
YELLOWTAIL	97%	98%	99%	99%	90%	91%	99%	99%
PERCHWUS	99%	99%	98%	98%	98%	99%	94%	100%
PERCHGOOSE	95%	96%	100%	100%	85%	86%	98%	98%
PERCHGA	84%	85%	97%	97%	73%	73%	87%	87%
PERCHAI	90%	90%	100%	100%	78%	79%	93%	95%
PERCHEBS	98%	97%	99%	99%	90%	89%	99%	99%
Average	95%	96%	99%	99%	87%	89%	96%	97%

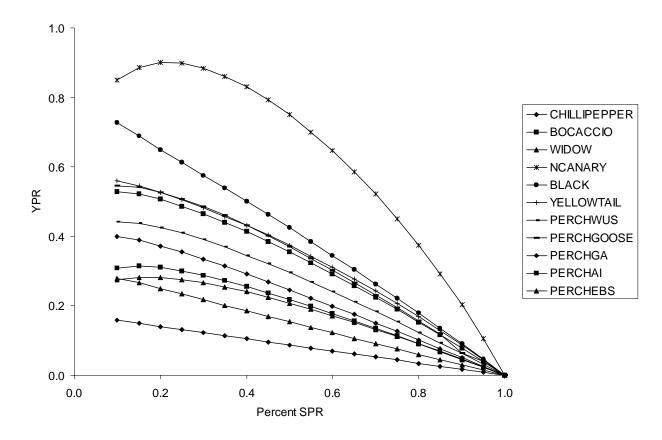


Figure 1. Yield per recruit (YPR) as a function of the percent unfished SPR for 11 eastern Pacific rockfish stocks.

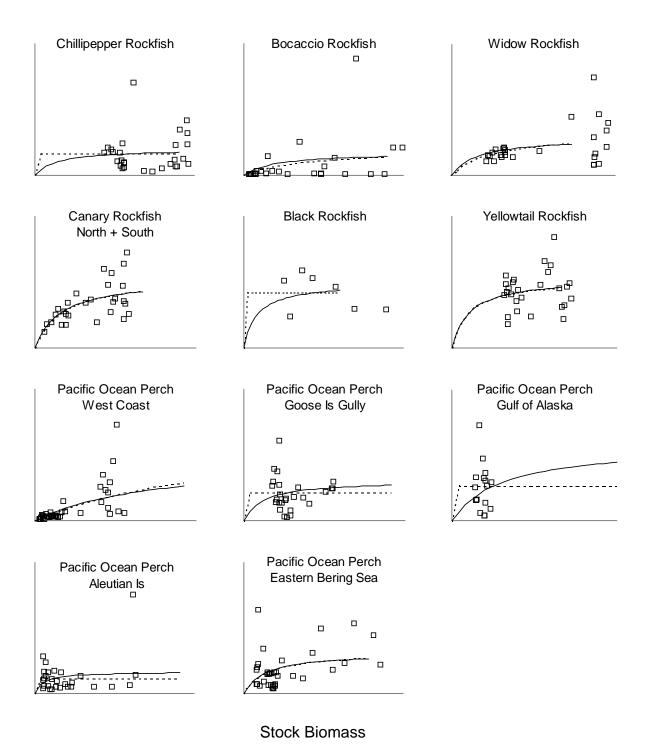


Figure 2. Stock recruit data for 11 eastern Pacific rockfish stocks. Two stock recruit curves are shown. The solid lines show the Beverton-Holt S-R curve based on the posterior mode from a Bayes hierarchical model. Dotted lines show the resulting curves when each S-R relationship is estimated separately.

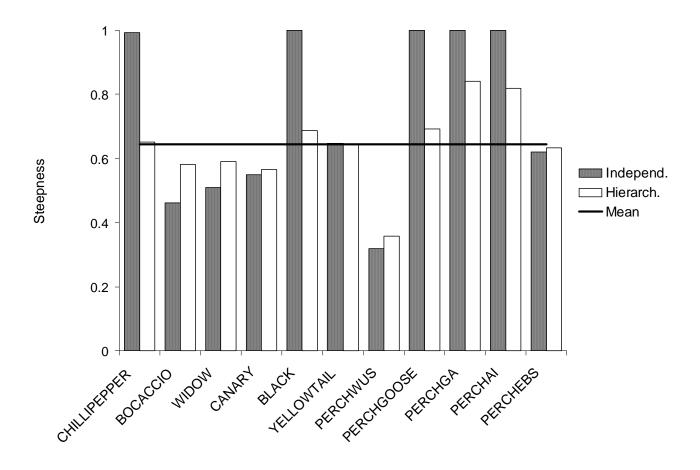


Figure 3. Posterior mode estimates of steepness, h_k , when each S-R relationship is estimated separately and for a Bayes hierarchical models for 11 eastern Pacific rockfish stocks.

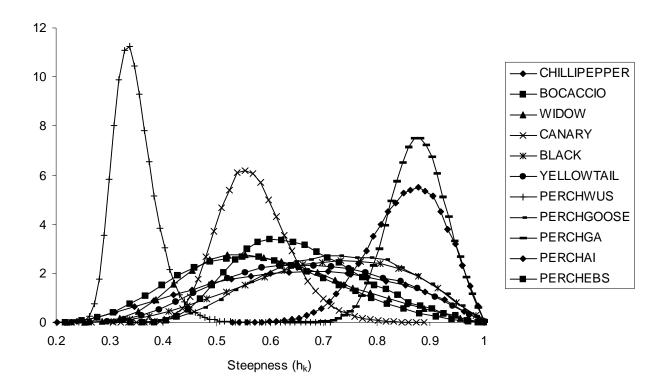


Figure 4. Marginal posterior distributions of steepness, h_k , for 11 rockfish stocks from a Bayes hierarchical model.

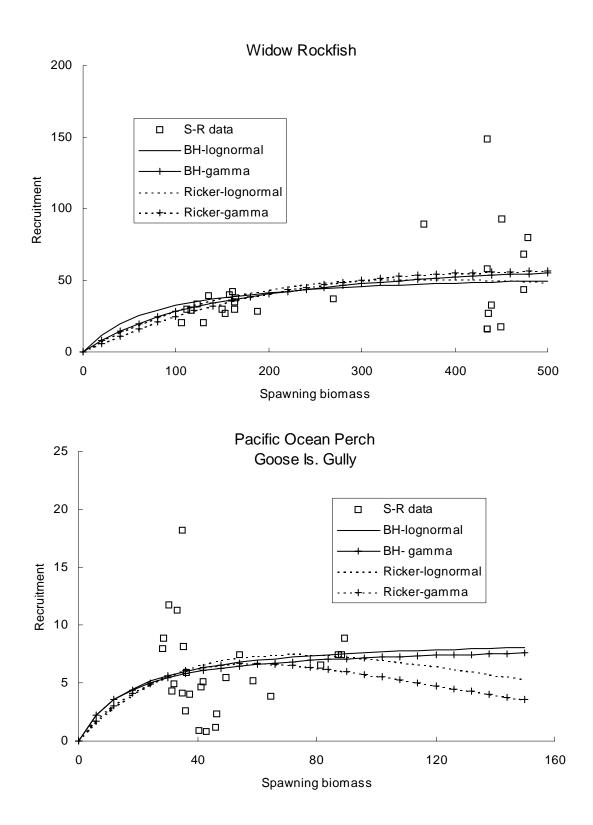


Figure 5. Comparison of posterior mode S-R curves for different stock-recruit models (Beverton-Holt and Ricker) and different recruitment error distributions (lognormal and gamma) for widow rockfish and Goose Island Gully Pacific Ocean perch.

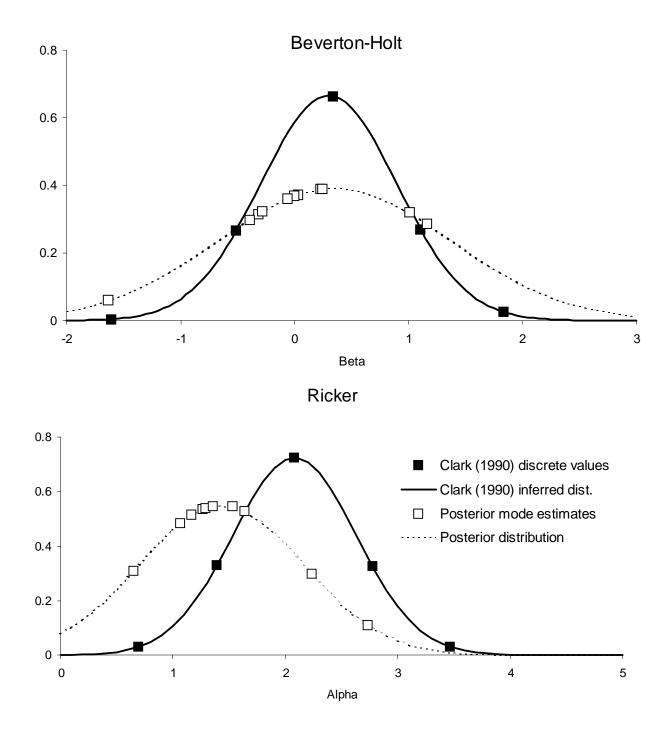
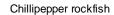
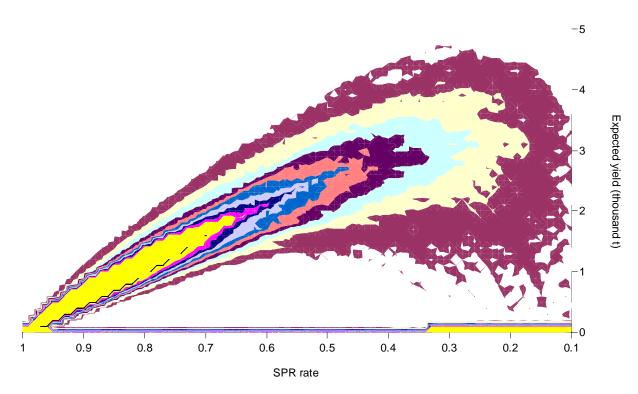
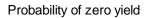


Figure 6. Posterior predictive distribution of β_k for the Beverton-Holt model for an unobserved stock (top panel). The location of the posterior mode estimates of β_k for ten rockfish stocks are indicated on the distribution. Also shown is a distribution inferred from the discrete Beverton-Holt S-R curves (points indicated on the distribution) considered by Clark (1990). The bottom panel shows the posterior predictive distribution of α_k for the Ricker model.







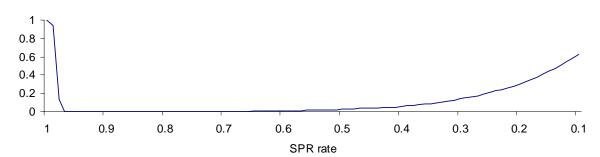


Figure 7. Distribution of equilibrium yield obtained by MCMC sampling as a function of the SPR harvest rate for chillipepper rockfish. The bottom panel shows the probability of zero yield.

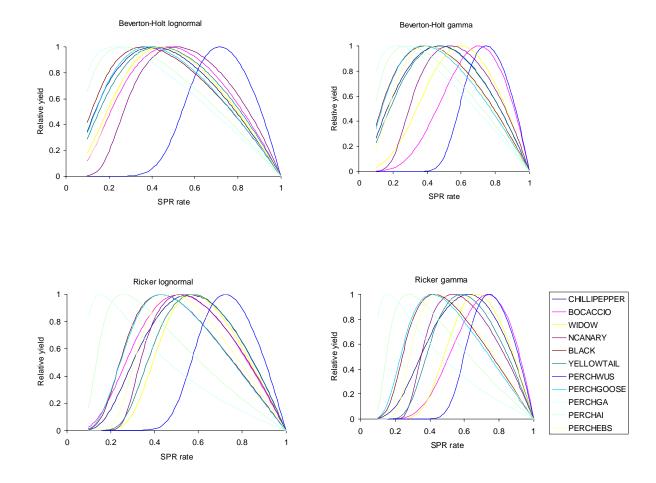


Figure 8. Relative expected equilibrium yield as a function of the SPR harvest rate for different S-R models (Beverton-Holt and Ricker) and different error distributions (lognormal and gamma) for ten rockfish stocks.

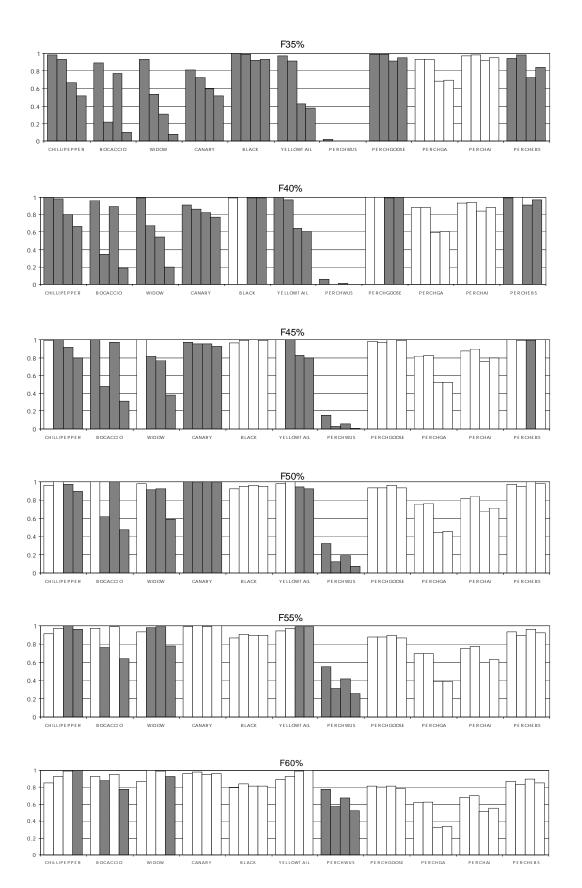


Figure 9. Relative expected yield at SPR harvest rates from F35%-60% for ten rockfish stocks. The results from four models are shown for each stock (from left to right: Beverton-Holtlognormal, Beverton-Holt-gamma, Ricker-lognormal and Ricker-gamma). Solid bars indicate that the harvest rate is higher than SPR rate that maximizes expected yield.